"New Investigations into the Reduction Phenomena of Animals and Plants.—Preliminary Communication." By J. B. Farmer, F.R.S., and J. E. S. Moore, A.R.C.S. Received May 29,—Read June 18, 1903.

The attention given by numerous investigators to those periodically recurring nuclear changes known as reduction divisions, has so far apparently resulted only in an increasingly wide divergence of opinion, both respecting the nature of the process and its significance, but there are nevertheless a number of cardinal facts upon which all are fairly agreed. It is generally admitted, for example, that during the reduction processes the number of the chromosomes is halved; that this is everywhere effected during the period of rest immediately proceeding the mitoses in question; that two consecutive mitoses appear to be intimately connected with this process, but the first of these, the heterotype division, is generally markedly distinct from other nuclear divisions; consequently it would seem probable that the explanation of the reduction in the number of the chromosomes, of reduction generally, is to be obtained through a minute study of the heterotype or synaptic prophase in a large number of animals and plants. With this conception before us, we have sought out in each case as complete and unbroken a series as possible, illustrating the stages by which the synaptic spireme thread is converted into the reduced heterotype chromosomes; and the results of our investigations have not only been such as to considerably modify the conception of the process as already set forth by ourselves in a number of former memoirs, but at the same time to indicate a possible reconciliation between most of the different views which have been and are held by other investigators.

The two main theories as to the nature of reduction may be shortly stated. In the first we have the process regarded as a qualitative *and* quantitative division of the chromatin by the ultimate separation into daughter nuclei of entire somatic chromosomes. It is assumed that such entire chromosomes may be temporarily united during the early prophase of the heterotype division, and thus a "pseudo-reduction" (Häcker) be brought about. But during the homotype division these chromosomes are separated and pass in their entirety to one or other of the daughter nuclei. It is held by most investigators that the final separation is effected during the second or homotype division, the heterotype being characterised by the separation of the longitudinally split halves of the chromatic thread-work.

The second view is that which was strongly urged by Brauer, and is now held by a large number of both zoological and botanical investigators. According to this conception the identity of the original somatic

chromosomes becomes lost at the close of the cycle preceding the synaptic rest; and they are replaced by half the somatic numbers of new ones which first become visible in the prophase of the heterotype division. During their formation these reduced chromosomes become longitudinally divided twice, in planes at right angles to each other, and in this way the frequently observed rapid succession of hetero- and homotype divisions is accounted for, the fission for both mitoses having taken place almost simultaneously. Many instances have been described of the synaptic chromosomes presenting the appearance of doubly split threads, and this second view of the reduction process consequently appears to rest upon quite as sound a basis of observation as the first. As they stand, the results of existing investigations upon these matters would appear to lead to a belief that the reduction processes are diverse in character and cannot possess the theoretical importance which it has been suggested may attach to them.

A re-investigation of the whole matter has, however, convinced us that neither of the above interpretations is correct. We find that the appearances, hitherto supposed by nearly all observers* to indicate the mode of formation of the heterotype chromosomes, do not seem to have been correctly apprehended, this being due to certain important stages in the process having escaped adequate appreciation. The entire metamorphosis is admittedly excessively difficult to observe, but the whole may be traced in a manner which seems to leave no room for doubt that both the appearance of a double longitudinal fission, and the origin of the heterotype daughter-chromosomes from split threads, are quite illusory. Moreover, in the numerous plants and animals in which we have followed out the process, we have obtained remarkably concordant results, and we think that the explanation we are now able to give of the origin of the reduced chromosomes is one which incidentally accounts for the many peculiar figures and vagaries that have so frequently been observed and remarked upon.

At the end of the synaptic rest, that is, in the prophase of the heterotype division, the spireme thread certainly undergoes a longitudinal fission (Figs. 1 and 2), often before it segments into the reduced number of chromosomes (Osmunda, Lily, Aneura, among plants; Salamander, Axolotl, Blatta, among animals). Following, however, upon this fission, which may result in a wide divarication of the longitudinal halves of the split thread work, comes a stage when the

* Schaffner, in 1897 ('Bot. Gazette') suggested that in Lilium Philadelphicum the process of reduction is essentially identical with that described in this paper. The value of his correct observations was obscured by errors in other respects, and they have lain practically unnoticed, perhaps on this account.

Korschelt ('Zeit. Wiss. Zool.,' vol. 60, 1895) describes a peculiar process for Ophryotrocha that is easily brought into line with our observations, though hitherto it has been regarded as an isolated and peculiar case.

spireme contracts, and, as this phase progresses, the threads are pulled into more and more parallel positions (Figs. 2 and 3); and, if polarisation is strongly marked, as in most animals, the threads are seen to take the form of loops, or large U-shaped figures. Although still showing longitudinal fission, the sides of these loops approximate once more, and eventually nearly all signs of the original split are obliterated. But, even at a later stage, careful search often reveals the original opening running along the sides of the loops. This method of formation of the U-shaped chromatin bands, and the final approximation of their limbs, has given rise to a complete misunderstanding of the ensuing phases; the approximated limbs of the loop having been regarded as the longitudinally split halves of the spireme thread, and the great increase in their thickness having been supposed to be due to a large contraction in the length of the spireme.

The full sequence in the production of the loops can only be made out in very carefully prepared material, and as a result of a comparison of sections with uncut cells. The chromatin, indeed, during these stages seems to be in a condition very sensitive to unfavourable manipulation, and we have reason to think that the quite unnecessary length of embedding processes so frequently resorted to may be greatly responsible for the failure to recognise the true sequence of events. Every cytologist who has examined thick sections, or uninjured cells, in which the early heterotype chromosomes are shown, must have been struck with the appearance of forms composed of rods, often twisted on themselves with their limbs open at one end, and forming at the other a conspicuous loop, such loops being in reality nothing more than the bent middle portions of the original U-shaped spireme segments (Fig. 4). The bent portions of the loops, however, mark the place at which, during the metaphase, the heterotype loop will break apart into the two chromosomes, of which it is composed. It sometimes happens that, even at this stage, traces of the longitudinal fission can be distinctly seen, and it is the persistence or reappearance of this fission which has been taken for a second longitudinal split. The number of the chromatic loops corresponds to the reduced number of the chromosomes, and thus there is direct evidence that each loop is really bivalent in the sense in which the term was used by Häcker, but our view of the actual process of the formation of the loops, and of the subsequent course of events, does not coincide with the conclusions reached by this investigator.

When the bivalent chromosomes, loops or rings, become arranged on the spindle (Fig. 5), they split asunder in such a way that one limb of the loop passes into each daughter nucleus, and consequently it will be apparent that their division cannot be regarded as the completion of any longitudinal fission, but as a transverse separation of the chromosomes originally united together end to end in the bivalent loop ring or rod

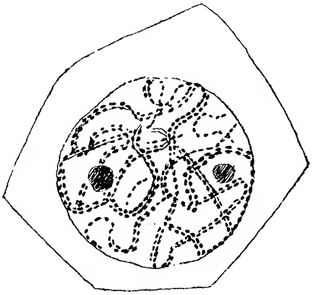

Fig. 1.

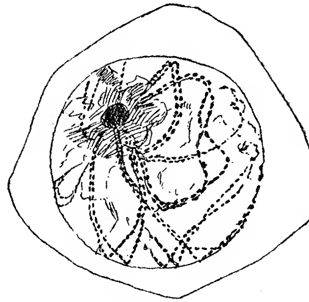

Fig. 2.

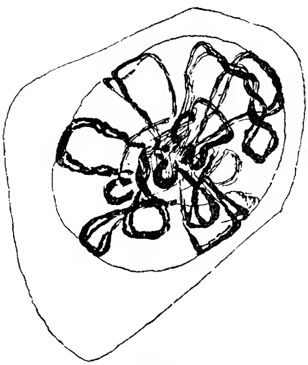

Fig. 3.

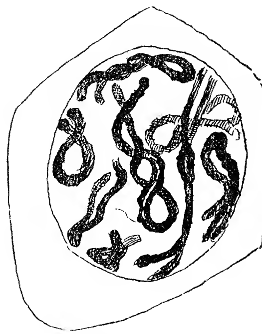

Fig. 4.

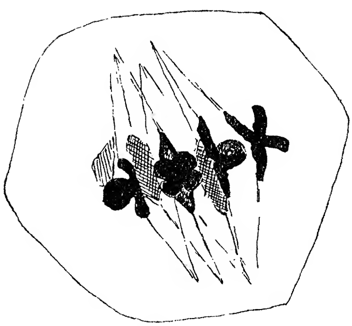

Fig. 5.

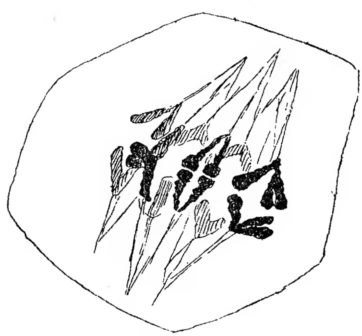

Fig. 6.

In Blatta,* the original longitudinal split is, as we have said, apparent

* The investigation of spermatogenesis in this insect was undertaken by Mr. L. Robinson, in conjunction with ourselves. His results will be presented in the final memoir.

while the rings are opening out on the spindle and before the united chromosomes of which it is composed have separated, and although in some cases it is more or less concealed, this early fission rapidly reappears, and the remarkable figures seen in the anaphases of Tradescantia or Salamander, thus find their explanation.

The deceptive appearances presented by lilies at this period also find an intelligible explanation when the mode in which they are attached to the spindle fibres is borne in mind, and a remarkable confirmation of this is forthcoming in the fact, which seems to have hitherto escaped observation, that in some cases the daughter-chromosomes, like those of Tradescantia, clearly show their original longitudinal split (Fig. 6). This original longitudinal fission of the spireme thread which is usually visible in the retreating daughter elements is retained in some, probably in all, cases as a preparation for a succeeding homotype division.

It would thus appear from the preceding observations, that the synaptic rest, culminating in the heterotype mitosis, is a phase specially intercalated in the reproductive cycle. In it a reduction of the number of the chromosomes is brought about by their adhesion in pairs, but with the inception of karyokinetic activity the spireme thread undergoes the longitudinal fission characteristic of ordinary somatic division, although the actual separation of these longitudinal halves is deferred until the next mitosis. Thus the heterotype division not only seems to be different in kind from an ordinary mitosis, but in this very fact probably lies the reason of the extraordinary diversity of form so often obvious among the chromosomes in this, as compared with any other, type of nuclear division.

We have purposely refrained in this communication from criticising the results of others, and from discussing the general bearings of our own interpretation of the phenomena upon heredity and other matters. We have done so because we think this part of the subject will find a more appropriate place in a memoir now in preparation, wherein the evidence for our conclusions will be fully set forth.

The illustrations that accompany this paper are intended merely to serve as diagrams explanatory of the more important stages of the heterotype division.

EXPLANATION OF THE FIGURES.

1. Spireme thread showing longitudinal fission.
2. Looping together of the split spireme.
3. Same at a later stage.
4. The loops have separated, and the longitudinal fission cannot always be recognised.

5 and 6. Stages in the separation of the daughter-chromosomes at the equatorial plate.